

SHELL REDUCTION AND LOSS IN FISSURELLIDS: A REVIEW OF GENERA AND SPECIES IN THE *FISSURELLIDEA* GROUP

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ABSTRACT

Six species in three related genera, the *Fissurellidea* group, have a hypertrophied development of the mantle covering the head and foot, a broad rachidian tooth, and the shell vestigial or lacking.

Fissurellidea Orbigny, 1841, has a radially striate shell and comprises the type species *F. megatrema* Orbigny, 1841, in southern Argentina, *F. patagonica* (Strebel, 1907) in southern Chile and southern Argentina, and *F. bimaculata* Dall, 1871, in the northeastern Pacific. *Megatebennus* Pilsbry, 1890, proposed originally for the latter, is synonymized with *Fissurellidea*.

Pupillaea Sowerby, 1835, differs from *Fissurellidea* in having a higher shell profile and in having two shell layers offset at the margin. It comprises the type species *P. aperta* (Sowerby, 1825) in South Africa, and *P. annulus* (Odhner, 1932) in southern Chile. The latter has a ringlike shell, an extreme vestige.

Buchanania onchidioides Lesson, 1830, from southern Chile, here reported for the first time since its description, lacks a shell as an adult, but is otherwise like other members of the *Fissurellidea* group; it has a groove in which there is probably a shell in early stages. This genus completes the trend toward shell reduction in the tribe Fissurellidini.

Although shell reduction and loss is a prominent trend in opisthobranch and pulmonate gastropods, it occurs very infrequently in prosobranchs. Heretofore, a complete loss of shell has been known in prosobranchs only in the neritacean family Titiscaniidae.

In the Fissurellidae, a trend toward shell reduction and loss is evident in three genera here called the *Fissurellidea* group. These genera—*Fissurellidea* Orbigny, 1841, *Pupillaea* Sowerby, 1835, and *Buchanania* Lesson, 1830—differ from most other large-bodied fissurellids in having a thick, leathery mantle enveloping the head and foot. Species of *Fissurellidea* have a highly reduced, vestigial shell; one species of *Pupillaea* has an even more reduced shell; and the complete loss of the shell in the adult stage of *Buchanania* Lesson, 1830, is first reported here.

The taxonomy of genera and species comprising this group has been confused in the literature. All three genera are represented in the Magellanic faunal province, which encompasses southern Chile and southern Argentina. Field work in Chile in 1975, and in Argentina in 1978, enabled me to collect four of the relevant species and to resolve a number of pertinent problems. Here the genera are newly defined and the species, totaling six, are briefly treated, basing the classification on characters of shell morphology and external anatomy.

Abbreviations for museums mentioned in the text are: AMNH, American Museum of Natural History, New York;

LACM, Los Angeles County Museum of Natural History; MACN, Museu Argentino de Ciencias Naturales, Buenos Aires; NM, Natal Museum, Pietermaritzburg, South Africa; USNM, United States National Museum of Natural History, Washington, D.C.

In the descriptions that follow, the specimens mentioned were collected in the lower intertidal zone unless otherwise indicated. Measurements of shells and bodies are given in this order: length, width, and height. Latitude and longitude are given for localities in southern Chile and Argentina, where there are many islands, but latitude only is given where the coastlines are continuous. Except where noted, specimens of shells and bodies are illustrated with the anterior to the top.

Family FISSURELLIDAE Subfamily EMARGINULINAE

I follow the classification of Thiele (1929) in recognizing two subfamilies in the Fissurellidae: the Emarginulinae and Fissurellinae, basing the division upon a major distinction in radular characters.

The subfamily Emarginulinae, which appeared in the Mesozoic, has a rachidian of varying breadth and the massive outer lateral tooth is bicuspid. In contrast, the Cenozoic appearing Fissurellinae have a rachidian tooth narrow and

tapered at the tip and an outer lateral tooth with four cusps (except three in *Macrochisma* Sowerby, 1839).

I subdivide the Emarginulinae into tribes, as further treated in other work in progress.

Tribe FISSURELLIDINI Pilsbry, 1890

[ex Fissurellidinae]

DIAGNOSIS. Shell (if present) relatively low; apex resorbed in mature shells; foramen at summit, relatively large, bordered by discrete callus ring on interior surface; callus not truncate nor depressed posteriorly. Animal much larger than shell, not retractable within it. Muscle scar reduced, lacking inwardly directed hook-shaped process. Rachidian tooth of radula ranging from extremely broad to narrow; outer lateral teeth bicuspid.

INCLUDED GENERA. *Lucapinella* Pilsbry, 1890; *Leurolepas* McLean, 1970; *Fissurellidea* Orbigny, 1841; *Pupillaea* Sowerby, 1835; *Buchanania* Lesson, 1830.

Genera differ from those of the Diodorini, some genera of which also have large-bodied animals, in lacking, on the shell interior, a depression posterior to the callus ring that surrounds the foramen, and in lacking the hook-shaped process of the shell muscle that characterizes all other members of the Emarginulinae.

Lucapinella, which is not treated further here, has a relatively large shell compared to the size of the animal, and the head and foot are not fully covered by the mantle. The mantle of *Leurolepas* fully envelops the head and foot as in the *Fissurellidea* group of genera, but the rachidian is relatively narrow and the inner laterals are nearly equal in size to the rachidian. Earlier (McLean, 1970), I considered the monotypic *Leurolepas* to be a member of the Fissurellinae, but here assign it to the Fissurellidini because the enlarged outer laterals are bicuspid like those of other Emarginulinae.

EXCLUDED GENERA. Pilsbry (1890) intended the Fissurellidini (which he proposed at the subfamily level) to include *Megathura* Pilsbry, 1890, which also envelops the head and foot, though the shell remains relatively large. *Megathura* is here allocated to the tribe Diodorini because the muscle retains the inwardly directed hook-shaped process, a character not considered by Pilsbry. Such other large-bodied genera as *Cosmetalepas* Iredale, 1924, and *Mono-dilepas* Finley, 1927, do not envelop the head and foot; they also have the hook-shaped process to the muscle and are referred to the Diodorini. *Amblychilepas* Pilsbry, 1890, has quadricuspid outer laterals and is allocated to the Fissurellinae.

The *Fissurellidea* Group of Genera

GENERIC DISTINCTIONS. Genera are defined on shell characters: sculptured with radial striae in *Fissurellidea*, with sharply differentiated margin in *Pupillaea*, and the shell lost altogether in mature *Buchanania*.

SHELL CHARACTERS. The shell (where present) is saddle-shaped, with ends raised; sculpture consists of broad radial ribs; on the interior, the callus ring surrounding the foramen is narrow and there is a narrow raised border along the shell margin. The foramen is proportionately larger than in most other fissurellid genera.

Shells comparable to the size of the animal are known in small specimens, those with shell lengths about $\frac{1}{4}$ the length of large shells. With growth the size of the animals increases faster than the shell. The expansion of the foramen also increases at a proportionately faster rate than growth of the shell.

Juvenile shells of *F. bimaculata* resemble those of *Diodora*, still retaining the apical whorl posterior to the foramen at a length of 2.5 mm. Postlarval shells have not been identified, but are probably like those of *Diodora*, in which the foramen appears on the anterior slope of the shell and for a very brief period leaves a selenizone behind, as illustrated by McLean (1984, figs. 7C, 7D).

ANATOMY. Odhner (1932) compared internal anatomy in some of the species treated here (see the citations in the synonymies) and Rodrigo-Trigo (1930) detailed the anatomy of *Fissurellidea megatrema*. Ghiselin, et al. (1975) reported that "*Megatebennus*" *bimaculatus* and some other fissurellids have a crystalline style.

The hypertrophy of the mantle in the *Fissurellidea* group is a modification of the characteristic mantle edge of fissurellids. Stasek and McWilliams (1973) showed that the fissurellid mantle edge has three discrete folds: 1) the outer fold, which secretes and maintains contact with the shell edge, 2) the middle fold, which extends up above the shell edge and may envelop the shell without obliterating the sculpture, and 3) the inner fold, which extends down to envelop the foot and frequently the head of the animal.

In the *Fissurellidea* group, there is a strong development of the middle fold covering the shell and, a massive development of the inner fold that extends over the head and foot. The hypertrophied development of both folds causes the shell to be essentially internal. For the greater part of its length the mantle roof above the gills consists of the thickened middle fold with no shell support.

Exterior coloration varies in all species. Colors include yellow, orange, brown, gray, or black, often with radiating patterns of lighter mottling. Mantle color is unrelated to shell color. The living animals have the general appearance of large-bodied dorid nudibranchs.

Small or half-grown specimens of *Fissurellidea* may partially or completely retract the thin shell-enveloping middle fold, thereby exposing the shell. Preserved specimens of the same species may exhibit varying amounts of middle fold retraction [compare Figures 15 and 16]. When shells are removed from preserved specimens of *Fissurellidea* by cutting back the middle fold, the small, shell-secreting outer fold may be observed within the groove that marks the position of the shell.

The snout (Figs. 21, 33) is often concealed between

the foot and the inner fold of the mantle in preserved specimens.

RADULAR CHARACTERS. The radula of the *Fissurellidea* group is not unlike that of *Diodora* and other members of the tribe Diodorini. The rhomboid-shaped rachidian tooth characteristic of emarginuline fissurellids has its broadest expression in this tribe. In the adults of some species the rachidian may be three times as broad as high. However, the morphology of the central field (rachidian and inner laterals) in all fissurellids is not especially important because these teeth lack strong cutting edges. The major functioning teeth are the large, bicuspid outer laterals, sometimes called the "dominant" teeth. Expansion of the broad rachidian provides the means by which the necessary separation between the opposing dominant teeth can be achieved. Hickman (1981) showed that the strong asymmetry of the radular ribbon of all fissurellids is caused primarily by the need for opposing dominants to fold together, zipper fashion, when the radula is not in its feeding stroke.

Barnard (1963) noted that the breadth of the rachidian tooth increases with growth in *Pupillaea aperta*. Such changes with growth are also true of the *Fissurellidea* species. Hence, the relative breadth of the rachidian does not provide a reliable taxonomic character at the specific level.

HABITAT. All species of the *Fissurellidea* group occur on rocky bottoms in the low intertidal and sublittoral zones. They occur on undersides of rocks or beneath projecting ledges where there is a thick growth of such encrusting organisms as sponges and compound ascidians. None of the species can strongly adhere to the rock substratum; all may easily be detached when the animals are exposed at low tide.

Ghiselin et al. (1975) reported that the gut of "*Megatebennus*" *bimaculatus* contained sponge spicules and that specimens in laboratory aquaria fed upon compound ascidians. Miller (1968) showed that *Lucapinella callomarginata* (Dall, 1871) feeds on sponges.

DISTRIBUTION. The center of distribution for the *Fissurellidea* group is the Magellanic faunal province. Two of the three species of *Fissurellidea* occur there and the third occurs in the northeastern Pacific. *Pupillaea* has one species in the Magellanic province and another in South Africa. *Buchanania* has one species in the Magellanic province.

FOSSIL RECORD: Wenz (1938), followed by Keen (1960), indicated a European Eocene record for *Fissurellidea*. I have traced the record to *Fissurella minosti* Melleville, 1843, placed in *Fissurellidea* by Cossmann and Pissarro (1910-1913, pl. 2, fig. 7). However, I assign that species to the tribe Diodorini because the interior view given by Cossmann and Pissarro shows that the foramen is circular and the interior callus is truncate posteriorly. For the same reason, I also reject Wenz's Eocene subgenus *Pro-fissurellidea* as a member of the tribe.

Wenz (1938) erroneously reported a few ("wenige") species of *Pupillaea* in the Pliocene of "South America." I have traced the record to "*Pupillia aperta tehuelcha*" Ihering, 1907, which is here treated in the synonymy of *F. megatrema*.

Genus *FISSURELLIDEA* Orbigny, 1841

Fissurellidea Orbigny, 1841: 447. Type species (monotypy): *F. megatrema* Orbigny, 1841.

Megatebennus Pilsbry, 1890: 182. Type species (original designation): *Fissurellidea bimaculata* Dall, 1871.

SHELL. Small relative to size of animal, low, ovate-rectangular; ends raised relative to sides. Sculpture of broad, low ribs separated by narrow grooves. Foramen oval, very large; interior callus ring narrow. Muscle scar very narrow, close to shell margin; shell margin finely crenulated by radial sculpture, interior of margin with rounded, slightly projecting border. Color buff, with pattern of darker rays.

In gerontic specimens, growth may stop and the shell edge may become either thinner or thicker, or upwardly deflected. Such changes in the shell should have no important effect because the shells have little functional significance.

MANTLE. Length of body 3 to 7 times shell length; mantle lobes thickened, enveloping shell and extending down to cover head and foot.

RADULA. The breadth of the rachidian varies among the species from nearly equal to the height, to almost three times the height, but as discussed above, this serves only to keep the massive outer lateral teeth well separated.

REMARKS. Shells of *Fissurellidea* are flatter and do not have the offset margin of *Pupillaea*.

Species of *Fissurellidea* are: *F. megatrema* Orbigny, 1841, southern Brazil to southern Argentina; *F. patagonica* (Strebel, 1907), southern Argentina to southern Chile; and *F. bimaculata* Dall, 1871, northeastern Pacific. Distributions of the three species are shown in Figure 1.

SYNONYMY. *Megatebennus* Pilsbry, 1890, is here synonymized with *Fissurellidea*. Until now *Megatebennus* was used for its type species, *F. bimaculatus*, in the northeastern Pacific, and the Magellanic *F. patagonicus*. Pilsbry (1890:182) stated that *Megatebennus* differed from *Fissurellidea* "in the much greater proportional size of the shell, more elevated body, the foot (viewed ventrally) almost as extensive as the mantle, the margin of the latter not at all thickened, and the shell not white-bordered above." However, Pilsbry's knowledge of the type species of *Fissurellidea* was based on misleading accounts in the literature. The white-bordered appearance to the shell of *F. megatrema* in Orbigny's original illustration, which was regarded as significant by Pilsbry, is a possible gerontic expression, not a character of generic importance. Orbigny's figure of the animal of *F. megatrema* is also misleading in showing a flattened body. The proportional size distinctions claimed by Pilsbry are not sustained here. None of Pilsbry's comparisons serve to separate *F. bimaculata* from the two species occurring in South America.

The radula of *Fissurellidea bimaculata* has a rachidian tooth not as broad as that of the other two species, but this does not suffice for generic separation, considering how this character varies among species in other fissurellid genera.

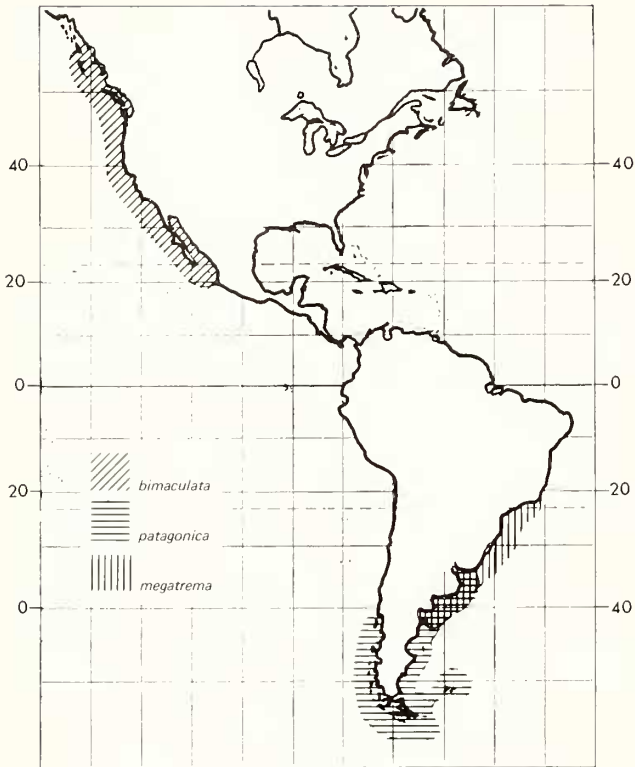


Fig. 1. Distribution of *Fissurellidea* species in North and South America.

***Fissurellidea megatrema* Orbigny, 1841**

Figures 2–9

Fissurellidea megatrema Orbigny, 1841: 477, pl. 63, figs. 5–10; Rodrigo-Trigo, 1930: 281 [anatomy].

"*Fissurellidea hiantula*." of authors: Pilsbry, 1890: 179–180, pl. 43, figs. 89–93 [copy Orbigny's figs. of *F. megatrema*]; Ihering, 1927: 103; Odhner, 1932: 294, figs. 26, 27 [anatomy], fig. 41.3 [radula], pl. 5, figs. 9–11 [shell]; Carcelles, 1944: 240, figs. 3–7; Carcelles, 1950: 50; Carcelles and Williamson, 1951: 253; Barratini and Ureta, 1960: 92; Castellanos, 1970: 17, pl. 1, fig. 6; Rios, 1975: 17, pl. 3, fig. 32; Figueiras and Sicardi, 1980: 180. Not *Fissurella hiantula* Lamarck, 1822, v. 6(2): 14.

Pupillia aperta tehuelcha Ihering, 1907: 399.

SHELL. Oval, thin; anterior slope slightly concave, elevating front margin. Sculpture of broad radial ribs, separated by incised grooves, concentric sculpture of growth increments, faintly rayed in gray or brown. Foramen elongate-oval, broader posteriorly, at least $\frac{1}{3}$ shell length in large shells, proportionately less in smaller shells. Margin finely crenulate at edge, interior with rounded, projecting border; margin of gerontic specimens often upturned, some

appearing white-bordered on upper surface due to cessation of pigmentation at shell edge.

Dimensions of large shell: $27.4 \times 19.4 \times 5.7$ mm (LACM 34932, Mar del Plata, Argentina).

MANTLE. Shell positioned at anterior third, body up to seven times length of shell; mantle surface thickened, usually with radiating rows of large swellings; overall color yellow, gray, or brown, with lighter colored large swellings, usually with dark pigmentation in fine reticulate pattern and scattered, irregular black markings midway on sides; some specimens gray or yellow overall with no apparent indication of large swellings.

Dimensions of largest preserved specimen: $71 \times 45 \times 25$ (LACM 34935, Mar del Plata, Argentina).

Preserved specimens usually have the middle fold of the mantle partially retracted, exposing a small area of the shell surface.

RADULA. Rachidian tooth broad, 2 to 3 times as broad as high (Fig. 5).

DISTRIBUTION AND OCCURRENCE. Rio de Janeiro, Brazil ($22^{\circ}53'$ S) (Rios, 1975), south to Punta Ninfa, Chubut Province, Argentina ($43^{\circ}21'$ S) (LACM). Occurring offshore in Brazil and Uruguay. At Mar del Plata, Argentina, and to the south, also occurring in the intertidal zone on undersides of rocks and overhanging ledges.

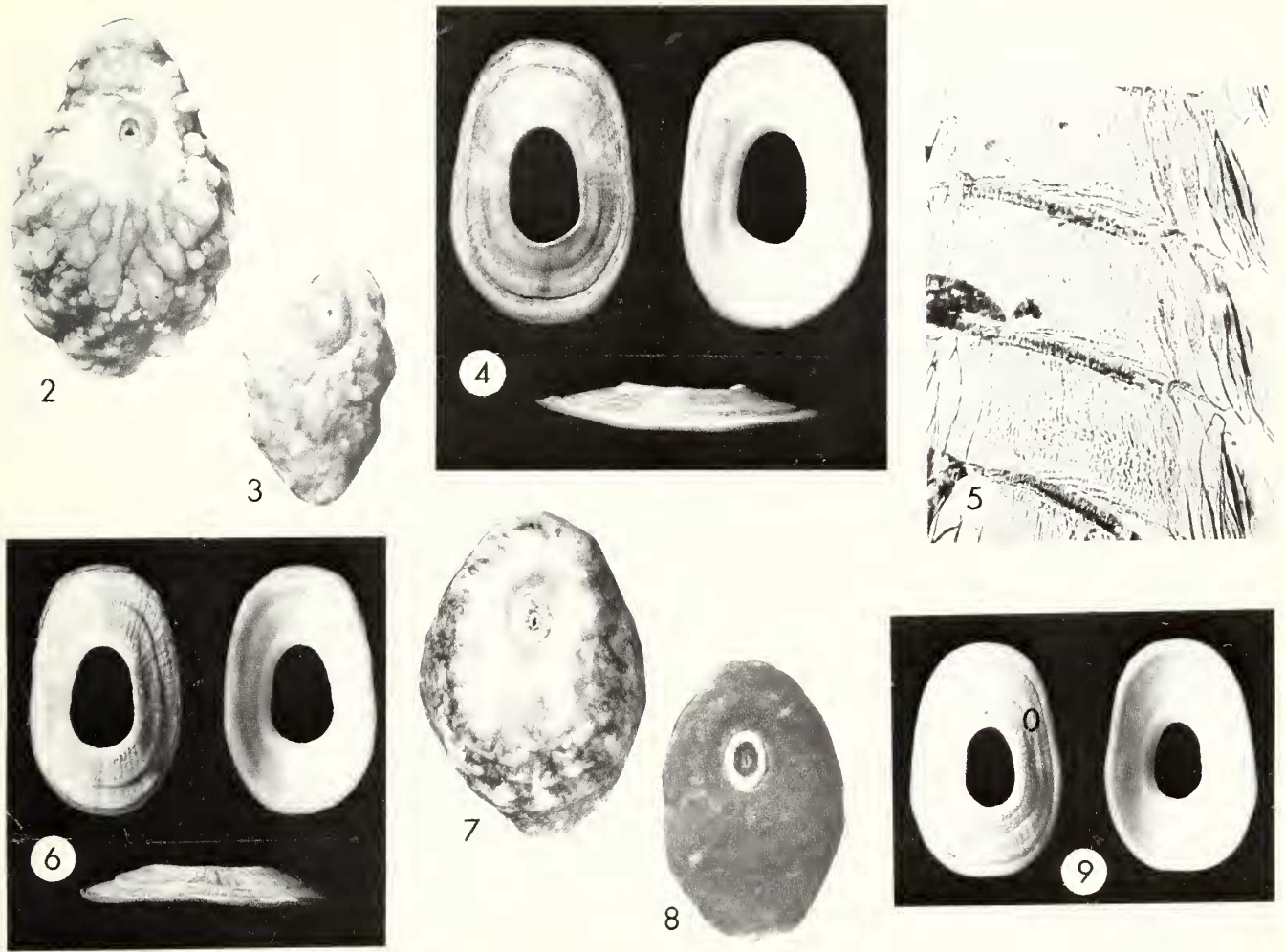
TYPE MATERIAL AND LOCALITY. I examined two syntypes of *Fissurellidea megatrema* in the Paris Museum in August 1980. Type locality: Ensenada de Ros, [15 "leagues" S of] Rio Negro, Argentina [approximately 41° S].

MATERIAL. LACM, 20 lots, intertidal zone, from numerous localities in the vicinity of Mar del Plata, Buenos Aires Province, Argentina, collected by C. J. Risso-Dominguez, 1964–1973. LACM, 2 lots, intertidal and dredged offshore, Golfo Nuevo, Chubut Province, Argentina, collected by J. H. McLean on R/V HERO, July 1978. LACM, 45–55 m, S of Punta Ninfa, Chubut Province, Argentina, J. H. McLean on R/V HERO, July 1978.

COMPARISONS. The mature shell of *Fissurellidea megatrema* (Fig. 4) is broader and more oval than that of the other two species and the foramen is larger and broader posteriorly, and proportionately the largest among the three species. The radiating rows of swellings in the mantle surface are characteristic, not shared by the other species, though *F. bimaiculata* has small tubercles in a similar radiating pattern.

SYNONYMY. Orbigny's illustration of *F. megatrema*, which were copied by Pilsbry (1890), show the mantle with a smooth gray surface and a shell with a white border. As mentioned above, the white bordered appearance of the type figure is not considered a generic or even specific character. The foramen in the original illustration is sufficiently large to dispel any possibility that it was based on the species identified here as *F. patagonica*. The shell figured by Orbigny is clearly conspecific with those illustrated here as *F. megatrema*.

Orbigny's figure of the animal does not show radiating rows of large swellings nor the pattern of scattered clumps of



Figs. 2-9. *Fissurellidea megatrema*. **Fig. 2.** Preserved specimen with shell intact, relaxed at fixation. Cabo Corrientes, Mar del Plata, Buenos Aires Province, Argentina (38° 01' S), C. J. Risso-Dominguez, February 1972. LACM 34935, 72 × 46.5 × 26 mm. **Fig. 3.** Small preserved specimen with shell intact. Punta Gruta, Mar del Plata, Argentina (38° 00.5' S), C. J. Risso-Dominguez, 11 April 1971. LACM 34934, 23 × 15 × 8 mm. **Fig. 4.** Shell, 55 m, Mar del Plata, Argentina (approximately 38° 00' S), A. Pinto, 1962. AMNH 147740, 27.8 × 18.1 × 4.0 mm. **Fig. 5.** Radular ribbon, light microscope preparation. Cabo Corrientes, Mar del Plata, Argentina (38° 01' S), C. J. Risso-Dominguez, February 1972. LACM 34936, horizontal width of field 0.8 mm, length of preserved specimen 44 mm, shell length 14.8 mm. **Fig. 6.** Shell, 45-55 m, S of Punta Ninfas, Chubut Province, Argentina (43° 15'-21' S), J. H. McLean, 17 July 1978. LACM 78-86, 17.7 × 10.9 × 3.1 mm. **Fig. 7.** Preserved specimen with shell intact. 20-50 m, between Punta Ninfas and Punta Cracker, Golfo Nuevo, Argentina (42° 54' S), J. H. McLean, 18 July, 1978 LACM 78-89, 61 × 42 × 29 mm. **Fig. 8.** Preserved specimen with shell intact. Same locality as Fig. 7. LACM 78-89, 45 × 29 × 21 mm. **Fig. 9.** Shell. Same locality as Fig. 6. LACM 78-86, 16.3 × 10.6 × 3.2 mm.

dark pigmentation characteristic of most specimens of this species. This would raise a serious question about the identity of Orbigny's material were it not for the fact that some freshly collected specimens do not show the usual pattern. Two specimens from the same haul in the Golfo Nuevo are shown in Figures 7 and 8. The specimen in Figure 8 is gray and has barely a trace of the swellings; the specimen in Figure 7 clearly shows the swellings. This demonstrates that the specimen illustrated by Orbigny is within the possible range of variation in this species.

Most previous authors have used the older name

Fissurella hiantula Lamarck, 1822, for this species. That assignment dates from Pilsbry (1890: 179), who stated: "This is unquestionably the true *hiantula* of Lamarck, agreeing with his description, and with the figure in Born's Test. Mus. Caes. Vindob., p. 414, vignette fig. F." No matter what the identity of the figure in Born (1778), which is further discussed below, Lamarck's reference to this figure must be discounted, because Mermod (1950: 708, fig. 18) located type material of *F. hiantula* in the Lamarckian collection. Mermod illustrated three specimens, none of which have foramina sufficiently large to be conspecific with *Fissurellidae megatrema*. Mer-

mod considered Lamarck's specimens to have come from South Africa; Kilburn and Rippey (1982: 35) have used the name in the combination *Amblychilepas scutellum hiantula* (Lamarck, 1822), for a South African species.

I have examined the vignette figure in Born (1778: 414) and am certain that it is based on the species here treated as *Pupillaea aperta*. The shell depicted has dark rays and a sharply defined white border; the foramen is not broader posteriorly, as expected in *F. megatrema*. Pilsbry's mistaken conviction that this figure represented the Argentinean species must have been the corroborating point that misled him to propose *Megatebennus*, for which the major justification was the supposed lack of the white border.

"*Pupillia aperta tehuelcha*" Ihering was based on an unillustrated Pliocene specimen from the Araucanian Formation at Sierra Laziar, Argentina. Ihering used the generic and specific combination because he incorrectly considered *F. megatrema* a synonym of the South African *Pupillaea aperta*. The only difference from the living Argentinian species, with which he compared it, was that the radial sculpture was slightly stronger ("un peu plus forte"). In the absence of an illustration, the name is retained in the synonymy of *F. megatrema*, in keeping with Ihering's intentions.

Fissurellidea patagonica (Strebel, 1907)

Figures 10–18

Megatebennus patagonicus Strebel, 1907: 98, pl. 2, figs. 23a–f; Strebel, 1908: 79; Melvill and Standen, 1914: 116; Odhner, 1932: 294, figs. 22–25 [anatomy], fig. 41.4 [radula], pl. 5, figs. 4, 5 [whole animal]; Riveros-Zuñiga, 1951: 133, fig. 37; Powell, 1951: 85; Carcelles, 1950: 50, pl. 1, fig. 8; Carcelles and Williamson, 1951: 253; Dell, 1971: 193; Figueiras and Sicardi, 1980: 180.

SHELL. Elongate-oval, thin to moderately thick. Sculpture of broad radial ribs, separated by incised grooves; concentric sculpture of growth increments, shells faintly rayed in gray or brown. Anterior and posterior ends slightly raised. Foramen elongate-oval, $\frac{1}{4}$ to $\frac{1}{3}$ length of shell. Margin finely crenulate at edge, interior with rounded, projecting border; gerontic specimens may have thinner shells at margin.

Dimensions of large shell: 27.5 × 15.6 × 5.9 mm (Fig. 10).

MANTLE. Shell positioned at anterior third, body up to 4 times length of shell; mantle surface thickened, pustules or tubercles lacking; color brown, black, or gray, some mottled, with lighter areas in a radiating pattern (Fig. 11).

Dimensions of large preserved specimen: 70 × 50 × 32 mm (Fig. 15).

The shell is but slightly exposed in undisturbed living specimens; that in Figure 11 is a living specimen in a dish of sea water in which the mantle has retracted to expose the shell, as in preserved specimens. Figures 15 and 16 show two preserved specimens from another locality, one of which (Fig. 16) did not retract the middle fold to expose the shell.

RADULA. Rachidian tooth $1\frac{1}{2}$ times broader than high (Fig. 18).

DISTRIBUTION AND OCCURRENCE. Uruguay (Figueiras and Sicardi, 1980), south to Tierra del Fuego, and the Falkland Islands; north in Chile to at least Pargua, Llanquihue Province (41° 47' S) (LACM). Rocky intertidal and sublittoral zones, not uncommon.

TYPE MATERIAL AND LOCALITY. According to Dance (1966), the Strebel Collection was destroyed in World War II. Type locality: Lennox Island, SE of Tierra Del Fuego, Argentina.

MATERIAL. LACM, 4 lots, intertidal and sublittoral in the Gulf of Corcovado, at Pargua, Pumalin, and Islota Nihuel, Chiloe Province, Chile, collected by J. H. McLean, November 1975. 1 lot, intertidal, Puerto el Hambre, Strait of Magellan, Magallanes Province, Chile, J. H. McLean, November 1975. LACM, 4 lots, 5–20 m, vicinity of Isla de los Estados, E of Tierra del Fuego, Argentina, collected by P. Dayton on R/V HERO, November 1972 and May 1973. LACM, 1 lot, Bahía Laura, Santa Cruz Province, Argentina (ex MACN). MACN, 1 lot, Punta Norte, Peninsula Valdez, Chubut Province, Argentina (Fig. 13).

COMPARISONS. The shell of *Fissurellidea patagonica* is narrower than that of *F. megatrema* and the foramen proportionately smaller and more elongate. Shells are less concave on the anterior slope than in *F. megatrema*. The mantle surface differs in lacking the regular swellings and concentrated, darkly pigmented areas of that species. The shell is relatively larger compared to overall body size than in *F. megatrema*.

REMARKS. Strebel, followed by later authors, placed this species in *Megatebennus*, no doubt because of the relatively large size of the shell compared to body size. However, the bodies of the large specimens from Isla de los Estados, Argentina (Figs. 15, 16) are nearly as large as those of *F. megatrema*. One specimen (Fig. 12) even has a white appearing margin to the shell, as do some specimens of *F. megatrema*. The specimen in Figure 17 is unusually thin-shelled.

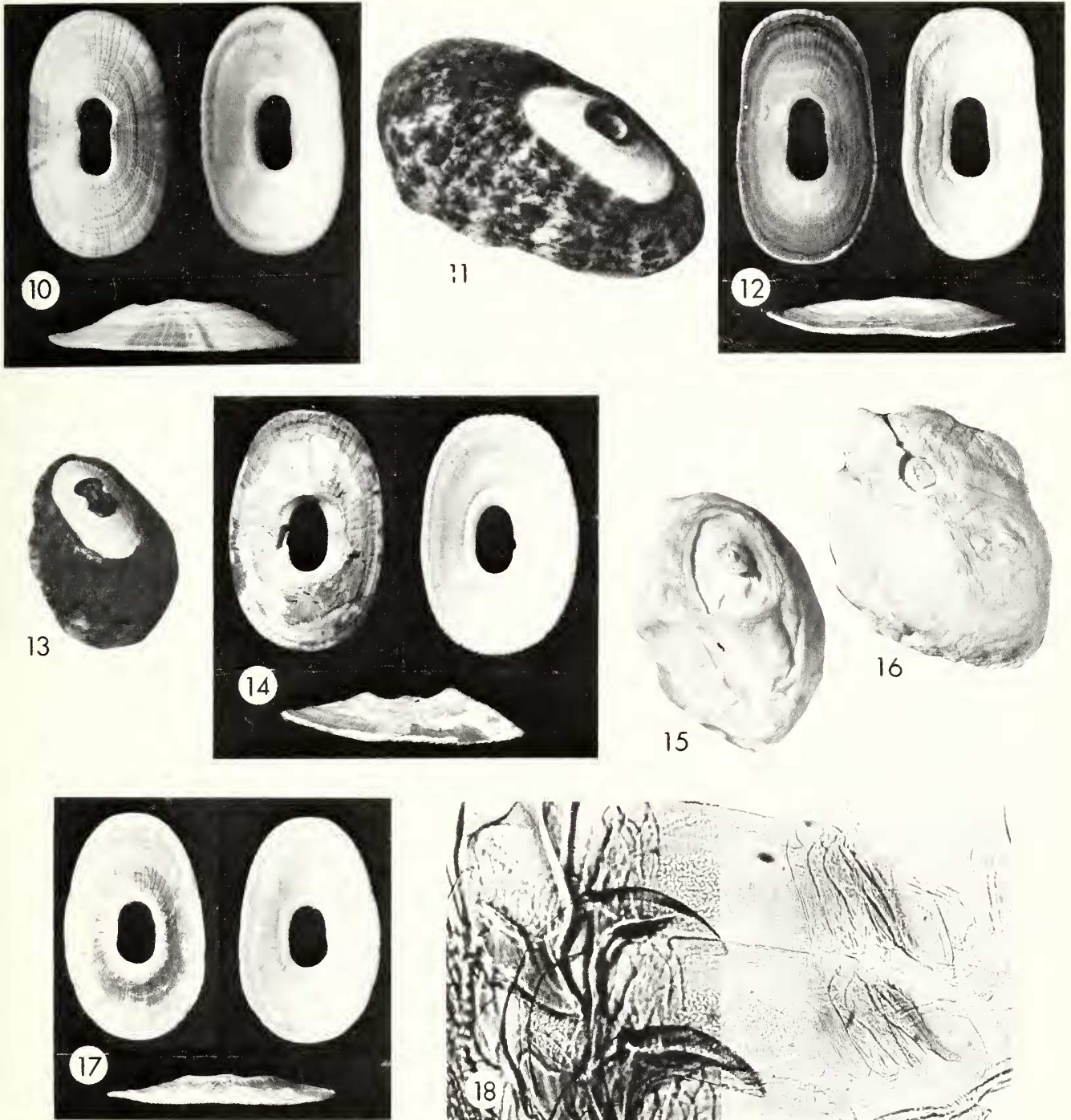
Fissurellidea bimaculata Dall, 1871

Figures 19–25

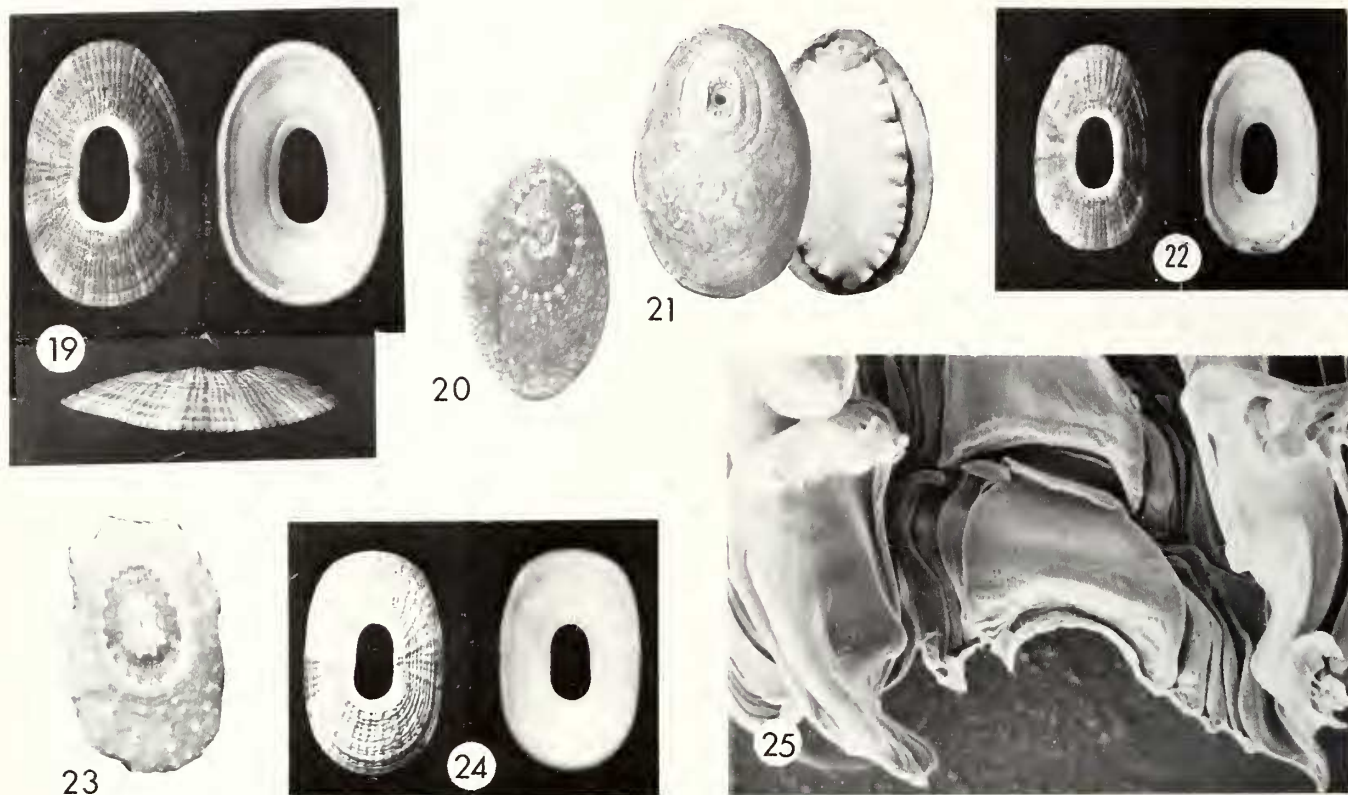
Fissurellidea [sic] *bimaculata* Dall, 1871: 132, pl. 15, fig. 7. *Megatebennus bimaculatus*, Pilsbry, 1890: 183, pl. 44, fig. 94, pl. 61, figs. 10–12; McLean, 1978: 14, fig. 3.5.

SHELL. Elongate-oval, moderately thick, sides nearly parallel, anterior slightly narrower than posterior; ends raised relative to sides; sculpture of broad radiating ribs separated by deeply incised grooves; concentric sculpture of lamellar growth lines. Color light brown, rayed with gray or brown. Foramen central, $\frac{1}{3}$ shell length, constricted in middle. Margin finely crenulate at edge, interior with rounded, projecting border.

Dimensions of large shell: 19.2 × 12.0 × 4.3 mm (Fig. 19).



Figs. 10–18. *Fissurellidea patagonica* **Fig. 10.** Shell. Isleta Nihuel, Golfo Corcovado, Chiloe Province, Chile (42° 38' S, 72° 57' W), R. T. Paine, 7 November 1975. LACM 75-44, 27.5 × 15.6 × 5.9 mm. **Fig. 11.** Living specimen, anterior at right, same locality as Fig. 10. LACM 75-44, dimensions of now contracted animal: 41 × 24 × 17 mm. **Fig. 12.** Shell. 10 m, Bahia Tom, Magallanes Province, Chile (50° 11.3' S, 74° 47.9' W), P. Dayton, 2 November 1972. LACM 72-158, 28.3 × 15.7 × 4.5 mm. **Fig. 13.** Intact preserved specimen. Punta Norte, Peninsula Valdez, Chubut Province, Argentina (42° 05' S). MACN 8367, length 33 mm. **Fig. 14.** Shell from specimen in Fig. 15. Intertidal, Isla Garrido, Aisen Province, Chile (45° 7.8' S, 74° 24.8' W), P. Dayton, 13 November 1972. LACM 72-162, 27.1 × 17.5 × 6.0 mm. **Fig. 15.** Preserved specimen with shell removed, same locality as Fig. 14 (shell in Fig. 14). LACM 72-162, 70 × 52 × 32 mm. **Fig. 16.** Preserved specimen, cut anteriorly to remove shell (shell in Figure 17). Same locality as Fig. 14. LACM 72-162, 62 × 41 × 28 mm. **Fig. 17.** Shell from specimen in Fig. 16. LACM 72-162, 24.9 × 15.4 × 2.8 mm. **Fig. 18.** Radular ribbon, light microscope preparation. Pargua, Canal de Chacao, Llanquihue Province, Chile (41° 47' S, 73° 28' W), J. H. McLean, 3 November 1975. LACM 75-30, horizontal width of field 1.5 mm, shell length 19.2 mm.



Figs. 19–25. *Fissurellidea bimaculata*. **Fig. 19.** Shell. Albion, California (39° 14.5' N), J. H. McLean, 11 November 1962. LACM 62-15, 19.2 × 12.0 × 4.3 mm. **Fig. 20.** Preserved specimen with intact shell. Pt. Dume, California (34° 00' N), D. Cadien, 8 February 1971. LACM 71-37, 29 × 17 × 12 mm. **Fig. 21.** Preserved specimen with intact shell. Cayucos, California (35° 27' N), P. I. LaFollette, 11 December 1977. LACM 90795, 34 × 21 × 16 mm. **Fig. 22.** Shell, same locality as Fig. 19. LACM 62-15, 14.8 × 8.7 × 2.6 mm. **Fig. 23.** Preserved specimen relaxed and fixed in Bouin's fixative, shell dissolved. Carmel, California (36° 32.5' N), J. H. McLean, 14 October 1981. LACM 90805, 16 × 10 × 7 mm. **Fig. 24.** Shell. Bahia Adair, Sonora, Mexico (31° 20' N), E. Huffman, May 1935. LACM 31862, 8.7 × 5.6 × 2.1 mm. **Fig. 25.** SEM micrograph of radula, courtesy C. Hickman. Horizontal width of field 0.8 mm.

MANTLE. Body up to 3 times shell length; shell near anterior end. Mantle yellow, orange, red, gray, or brown; with rounded, projecting tubercles in radiating rows.

Dimensions of large preserved specimen: 33 × 22 × 13 mm (Fig. 21).

The middle fold of the mantle covers the entire shell in living specimens; in preserved specimens it retracts to partially expose the shell.

The smallest preserved juvenile specimen examined (LACM 90795) has a shell 3.5 mm in length; the apex is intact and the body is no longer than the shell.

RADULA. Rachidian tooth slightly broader (at base) than high (Fig. 25).

DISTRIBUTION AND OCCURRENCE. Dall Island, Southeastern Alaska (55° N), to Bahia Santiago, Colima, Mexico (19° 26' N). Fairly common south to at least Sacramento Reef, outer coast of Baja California, Mexico (30° N), from the intertidal zone to 30 m on undersides of rocks and overhangs. There are only two records further to the south: four specimens collected by E. Huffman at Bahia Adair,

Sonora, in 1935 (Fig. 24) and one specimen collected at Bahia Santiago, Colima, Mexico, by Laura Shy in December 1966 (Shy Collection).

TYPE MATERIAL AND LOCALITY. Holotype, USNM 59273; type locality, Monterey, California.

MATERIAL. 78 lots are represented in the LACM collection from localities south to Sacramento Reef, Baja California.

REMARKS. This is the smallest member of the genus. The radiating rows of tubercles are similar to those of *F. megatrema* (compare Figures 3 and 23), which inescapably leads to the conclusion that the two species are congeneric.

Genus *PUPILLAEA* Sowerby, 1835

Pupillaea "Gray," Sowerby, 1835: 2 [validated in synonymy].

Type species (monotypy): *Fissurella aperta* Sowerby, 1825.

Pupillia Gray, 1840: 114, 147 [name only, invalid emendation of *Pupillaea* Sowerby].

SHELL. Moderately elevated; outline ovate rectangular, ends raised relative to sides; radial sculpture very subdued; foramen oval, from $\frac{1}{3}$ to $\frac{1}{2}$ shell length, interior callus ring narrow, muscle scar very narrow; shell margin not crenulate, pigmented exterior layer of the shell sharply offset from the white inner layer; interior border of margin narrow, not strongly projecting.

MANTLE. Body of animal 3 to 5 times longer than shell; mantle lobes thickened, enveloping shell and extending down to cover head and foot.

RADULA. Rachidian tooth $1\frac{1}{2}$ to 2 times broader than wide.

REMARKS. The chief distinguishing feature of *Pupillaea* is the offset margin of the shell. Sowerby II (1862: 204) aptly described it: "The species . . . has the peculiarity of a depressed insertional rim, resembling that by which the valves of a *Chiton* are inserted into the surrounding integument." The outer fold of the mantle, which secretes the growing edge of the shell, must also be significantly different from that of *Fissurellidea*.

Pupillaea further differs from *Fissurellidea* in having more subdued radial sculpture, and a higher and more steeply sloping profile.

Until now *Pupillaea* has been considered monotypic, regarded by many authors as a subgenus of *Fissurellidea*. Here the Chilean species described as *Fissurellidea annulus* Odhner, 1932, is also allocated to *Pupillaea*. Although the shell of the latter is reduced, it also has the offset margin, subdued radial sculpture, and steep profile of the type species. The significance of these characters would be difficult to evaluate were there but a single species, but the existence of two markedly disjunct species, provides an incontrovertible argument for generic recognition of *Pupillaea*.

SYNONYMY. Pilsbry (1890: 180) and Wenz (1938: 85) credited the genus to Krause, 1848. However, Keen (*in Moore*, 1960: 231), following Dall (1915: 439), correctly credited the genus to Sowerby, 1835, who unknowingly validated a manuscript name of Gray in synonymy. Sowerby's entry (1835: 2, pl. 2, fig. 10) was this: "*Fissurella hiantula*, Lam. Conch. Illust. f. 10. Southern Africa. Obs. For a representation of this species Lamarck refers to Born Vign. f. F. which is the same as I named *F. aperta* in the Tankerville Catalogue. The following are therefore synonyms of this species, viz. *Fissurella aperta*, Tank. Cat. app. p. vi, *Pupillaea aperta*, Gray in Supp. to Beechey's Narrative." As discussed above under *F. megatrema*, the Born figure is discounted as a "type figure." The Sowerby (1825) name for the species *aperta* is therefore valid. Lamarck's *F. hiantula* is now used for a South African species of *Amblychelapas* on the strength of original specimens in the Lamarckian collection.

Although Sowerby (1835) quoted a listing of *Pupillaea* in 1835, Gray's "Molluscos animals and their shells, in Beechey's Voyage . . ." was not to be published until 1839 (Gray, 1839), and a "*Pupillaea aperta*" was not included. As Dall (1915: 439), noted: "*Pupillaea* Gray also appears for the first time in the Conchological Illustrations, cited from the unpublished notes of Doctor Gray on the Mollusca of

Beechey's Voyage." Sowerby, however, is now the author of *Pupillaea*.

There is precedent for a familiar fissurellid genus validated in synonymy in the current usage of *Megathura* Pilsbry, 1890, which is now used for the large Californian *M. crenulata* (Sowerby, 1825). That generic name was first cited by Pilsbry (1890: 182) as "*Megathura californica* Nuttall MS." in the synonymy of "*Lucapina*" *crenulata*.

The synonym *Pupillia* Gray, 1840, was merely listed by Gray; no species were mentioned; the name must be considered an invalid emendation of *Pupillaea* Sowerby, 1835.

Fissurellidea and *Pupillaea* are here considered separate genera. A classification that equates the two at the subgeneric level will have to use the older *Pupillaea* as the nominate genus.

Pupillaea aperta (Sowerby, 1825)

Figures 26, 27

Fissurella aperta Sowerby, 1825: vi; Reeve, 1849: fig. 39. "*Fissurella hiantula* Lamarck," of Sowerby, 1835: 2, pl. 2, fig. 10 [with *F. aperta* in synonymy]. Not *F. hiantula* Lamarck, 1822.

Pupillaea aperta, Krause, 1848: 62, pl. 4, fig. 11; Sowerby II, 1862: 204, pl. 9, figs. 228, 229; Pilsbry, 1890: 180, pl. 44, figs. 6–8, pl. 62, fig. 9; Odhner, 1932: 304, fig. 41-1 [radula].

Fissurellidea (Pupillaea) aperta, Barnard, 1963: 288, fig. 21e [radula].

Fissurellidea aperta, Tietz and Robinson, 1974: 48, pls. 48c [shell], 49 [living animal]; Kilburn and Rippey, 1982: 36, pl. 6, fig. 13.

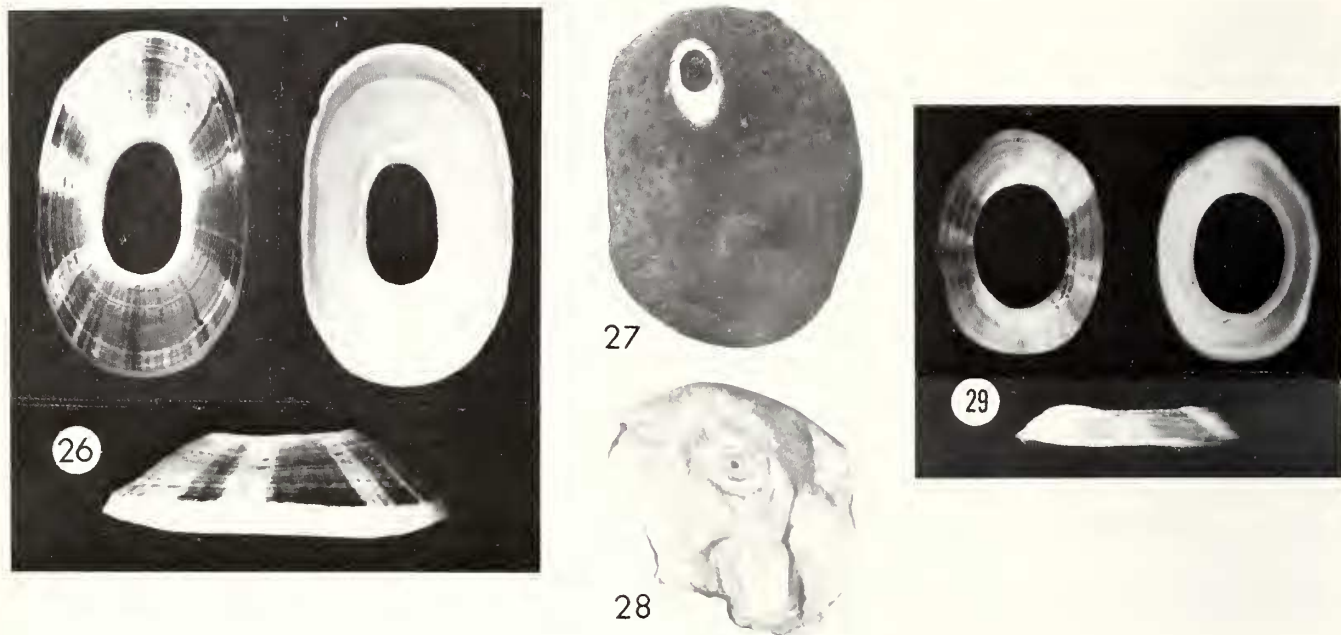
SHELL. Relatively large and thick, elongate-oval, sides steeply sloping, ends slightly raised; anterior slope longer than posterior and slightly concave, sides convex; ground color tan with dark gray rays. Sculpture of fine striae that form fine concentric lamellae under magnification. Foramen elongate oval, about $\frac{1}{3}$ length of shell. Outer shell layer sharply offset from broad, white inner layer; muscle scar narrow, interior with narrow projecting margin.

Dimensions of large shell: 39.0 × 24.4 × 10.3 mm (LACM 20206, Cape Town, South Africa). Maximum length 50 mm (Barnard, 1963).

MANTLE AND FOOT. Mantle enveloping shell, head, and foot. "Black or brown to orange in color, with the sole of the foot orange" (Kilburn and Rippey, 1982). Krause's illustration (copied by Pilsbry) indicates a mottled pattern similar to that of the *Fissurellidea* species. Tietz and Robinson (1974) illustrated a specimen with a fully enveloped shell and scattered dark colored protuberances on the mantle surface.

Dimensions of preserved specimen: 61 × 47 × 26 mm (Fig. 28). Largest preserved specimen: 110 × 80 mm (Barnard, 1963).

RADULA. Height of rachidian tooth about twice width



Figs. 26–27. *Pupillaea aperta*. **Fig. 26.** Beach worn shell. Strand, South Africa, D. W. L. Ackerman, January 1958. LACM 20246, 46.8 × 22.5 × 10.8 mm. **Fig. 27.** Intact preserved specimen. Intertidal, St. James, False Bay, South Africa. NM uncataloged, 61 × 47 × 26 mm. **Figs. 28–29.** *P. annulus*. **Fig. 28.** Preserved specimen with shell removed. Mehuin, Valdivia Province, Chile (39°23' S), J. H. McLean, 31 October 1975. LACM 75-36, 42 × 32 × 16 mm. **Fig. 29.** Shell of specimen in Fig. 28. LACM 75-36, 10.1 × 7.7 × 1.7 mm.

at base (according to illustrations of Odhner, 1932, and Barnard, 1963); outer lateral tooth bicuspid. The rachidian is wider in the adult than in juveniles (Barnard, 1963).

DISTRIBUTION AND OCCURRENCE. Southern Africa, Namibia to Western Transkei, "lives on underside of submerged rocks in sandy crevices, at and below low-tide level" (Kilburn and Rippey, 1982).

TYPE MATERIAL AND LOCALITY. Type material was not recognized in the British Museum during my visit in September 1980.

MATERIAL. The LACM collection contains 6 shell lots and one specimen with dried animal, all from South Africa; three lots from the Natal Museum, Pietermaritzburg, have also been examined.

REMARKS. This is largest species in the *Fissurellidea* group; shells attain nearly twice the length of *F. megatrema*. The smallest shell examined (7 mm length, NM C.206) shows the offset margin. I expect that earlier juvenile stages will show an unmodified margin.

***Pupillaea annulus* (Odhner, 1932)**

Figures 28, 29

Fissurellidea annulus Odhner, 1932: 292, fig. 34 [anatomy], fig. 41.2 [radula], pl. 5, figs. 1–3 [whole animal]; figs. 6–8 [shell]; Carcelles and Williamson, 1951: 253 [checklist only].

SHELL. Small, ringlike, oval, outline irregular; length of foramen over half length of shell, all slopes slightly less than 45 degrees from horizontal. Radial sculpture subdued, concentric sculpture of irregular, raised growth lines. Ground color buff, with lateral rays of gray. Margin sharp, not crenulated, offset from inner, white layer by angular groove.

Dimensions: 10.1 × 7.7 × 1.7 mm (Fig. 29); 13.5 × 9 × 1.5 mm (holotype).

MANTLE. Mantle enveloping shell, head, and foot. Surface of preserved specimen mostly smooth; color gray, with finely reticulating darker lines.

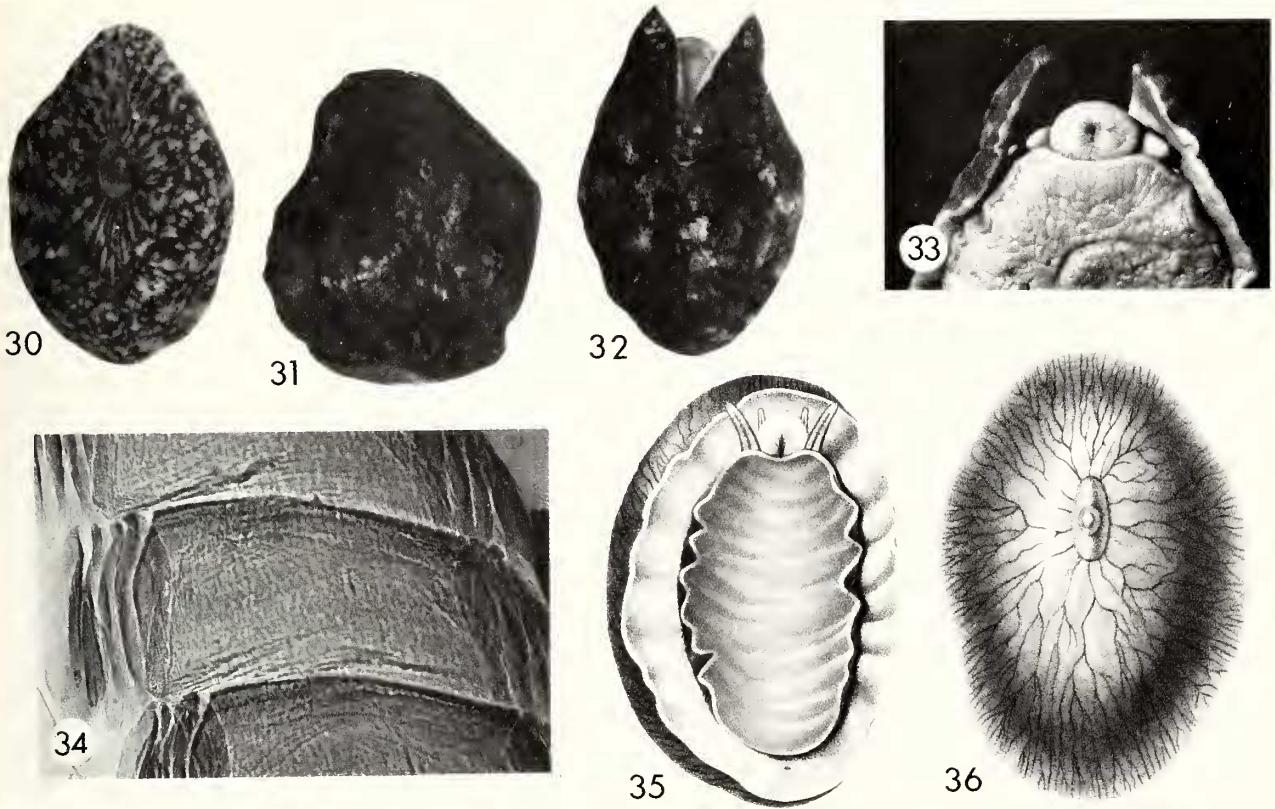
Dimensions of preserved specimens: 42 × 32 × 16 mm (Fig. 28); 72 × 63 × 35 mm (holotype).

RADULA. Rachidian tooth (as figured by Odhner, 1932) 1½ times broader than high; outer lateral tooth bicuspid.

DISTRIBUTION AND OCCURRENCE. Mehuin, Valdivia Province (39°23' S) (LACM 75-36), to Melinca, Chiloe Province, Chile (43°54' S) (type locality), rocky intertidal to 23 m. This species undoubtedly has a broader distribution in the Magellanic faunal province.

Chilean biologists have recently recognized this species in the fauna of southern Chile. Duarte, et al. (1980: 158) included it (as "*Fissurellidea*" *annulus*) in a study of caloric values among invertebrates from Valdivia, Chile (39°52' S).

TYPE MATERIAL AND LOCALITY. Holotype, Uppsala collection. 23 m, Melinca, Islas Guaitecas, Chile (43°54'



Figs. 30–35. *Buchanania onchidioides*. **Fig. 30.** Preserved specimen. Isla Laitec, Chiloe Province, Chile (43° 14' S, 73° 36' W), J. H. McLean, 9 November 1975. LACM 75-47, 42 × 27 × 16 mm. **Fig. 31.** Preserved specimen, same lot as Fig. 30. LACM 75-47, 42 × 30 × 15 mm. **Fig. 32.** Preserved specimen, mantle cut anteriorly to demonstrate absence of shell, same lot as Fig. 30. LACM 75-47, 42 × 27 × 16 mm. **Fig. 33.** Ventral view of anterior of same specimen in Fig. 32, showing the gill tips lateral to the blunt cephalic tentacles on both sides of the snout. **Fig. 34.** Light microscope preparation of radular ribbon from specimen in Fig. 33. LACM 75-47, horizontal width of field 1.0 mm. **Fig. 35.** Copy of original illustration of Lesson (1830), ventral view; note large cephalic tentacles and gill tips projecting over snout. **Fig. 36.** Same, dorsal view.

S, 73°45' W), collected by P. Dusen, May 1897 (Odhner, 1932).

MATERIAL. LACM 75-36, one specimen, rocky intertidal, Mehuin, Valdivia Province, Chile (39°23' S), collected by J. H. McLean, 31 October 1975 (Figs. 28, 29).

REMARKS. Despite the greatly reduced shell, *Pupillaea annulus* has in common with the South African *P. aperta* the offset margin, steeply sloping sides, and subdued radial sculpture.

The ringlike shell of this species results from the slowing of growth at the margin, accompanied by a continued expansion of the foramen. Although small shells have not been seen, it is likely that they will have proportionately smaller foramina. The LACM specimen has a smaller foramen than the holotype, but is a smaller specimen overall; with further growth, the size of the foramen in this specimen would have increased.

Genus *BUCHANANIA* Lesson, 1830

Buchanania Lesson, 1830: 60. Type species (monotypy): *Buchanania ochidioides* Lesson, 1830.

Because this genus is monotypic, the generic and specific diagnoses and discussions are combined.

***Buchanania onchidioides* Lesson, 1830**

Figures 30–36

Buchanania onchidioides Lesson, 1830: 60, pl. 14, figs. 4, 4D; Baker, 1938: 86, 88 ["a nomen dubium"].

SHELL. Lacking in mature specimens but probably present in juvenile stages.

MANTLE. Mantle thickened, enveloping head and foot on all sides, excurrent siphon $\frac{2}{5}$ mantle length from anterior end. Elongate groove in mantle encircling foramen; groove extending $\frac{1}{6}$ length of body, 1 mm in depth, lacking shell-secreting outer fold of mantle. Tips of ctenidia extending same length as (retracted) cephalic tentacles; side of foot with numerous, stubby epipodial tentacles. Color gray-brown with lighter mottling.

Dimensions: $42 \times 27 \times 17$ mm (Fig. 32). Dimensions of original material: 80×68 mm (Lesson, 1830).

RADULA. Rachidian tooth twice as broad as high; outer lateral tooth bicuspid (Fig. 34).

DISTRIBUTION AND OCCURRENCE. Concepción, Concepción Province ($36^{\circ}42'$ S) (type locality), to SE end Isla Chiloe, Chiloe Province, Chile ($43^{\circ}14'$ S) (LACM) The species undoubtedly has a broader distribution in the Magellanic faunal province.

TYPE MATERIAL AND LOCALITY. Type material lost in the Paris Museum (Lesson, 1830). Type locality: Bahía Concepción, Chile, collected in February 1823.

MATERIAL. LACM 75-47, intertidal, Isla Laitec, off SE end Isla Chiloe, Chiloe Province, Chile, three specimens, collected by J. H. McLean, 9 November 1975 (Figs. 30-34). This is the only record subsequent to that of the two original specimens.

SYNONYMY. The identity of *Buchanania onchidioides* has remained a mystery until now, due primarily to the loss of the original specimens subsequent to the time that drawings were made on the expedition of the "Coquille." Based upon field notes and the illustrations (copied here, Figs. 35, 36), Lesson concluded that the specimens were related to "*Onchidia*," now the family Onchidiidae. His generic name honored F. Buchanan, author of the genus *Onchidium* in 1800.

Authors treating the Onchidiidae (for example, Baker, 1938) have carried the name in lists of taxa in the family, but have not recognized nor further discussed the Lesson species. The generic name has also been burdened with misspellings and unnecessary replacements (*Buchannia* Gray, 1847; *Buchanaania* Gistel, 1848, and *Ephadra* Gistel, 1848, "substitute" for the latter; see references in Baker, 1938).

The rarity of the Lesson's "Voyage autour du monde. . ." in library collections also helps explain how a carefully illustrated species could remain in limbo for over 150 years. Because few have access to the original description, I include here a complete translation of Lesson's account:

"It is only in a rather incomplete way that we mention this curious and unique mollusk, for which we sent two good specimens to the Paris Museum. In vain we have searched the anatomical collection with M. Laurillard, neither have we found it among the invertebrate animals preserved in alcohol, with M. Rousseau; they seem to have been misplaced. Only from notes taken in the field and a drawing of the animal made in life can we describe it for the researches of future travelers.

"*Buchanania* has the most in common with the on-

chidias, and some points in common with the doris and the phyllidias. Like the onchidias, it has a large mantle, in the form of a shield, covering the entire foot and covering the head. As in the doris, the anus is dorsal, and as in the phyllidias, the gills are formed of leaflets placed in festoons (or scallops) along the two sides of the foot. The body of the specimen that we have illustrated reaches almost 80 mm in length, and the width about 68 mm. Its form is oval, its upper surface is very convex and rugose; the mantle excessively thick and fleshy, covering most of the foot. The foot is oval, rounded and free at the extremity, smooth or slightly striated over its surface. The shield of the mantle is leathery, papillate, pierced a little in front of center by a round hole, situated in the center of an oblong depression. The mouth is round, open under a fleshy flap, bearing on each side two pointed tentacles, contracted, and rather short, and two smaller, less prominent upper lobes.

"This mollusk has its mantle of dark cinnamon red, streaked with reddish brown. The thickened edge is on the underside yellow, tinted with red, and the foot is a very bright orange."

"We found it in February, 1823, at low tide, on a reef exposed for about two hours, later to be covered by a thick mass of water. The submarine bank is located at the entrance of the vast Bay of Concepcion, Chile" (Lesson, 1830).

It is apparent from the above that Lesson was a careful observer. Had he had opportunity to examine the preserved specimens upon return to Paris, he surely would have lifted the mantle in front to identify the smaller pairs of tentacles as fissurellid gills. He had made note of the epipodial tentacles and had interpreted them as gills, though these are not shown in his illustrations. In the preserved specimen in Figure 33, the tips of the gills project to the same extent as the cephalic tentacles.

The groove that surrounds the foramen of *Buchanania onchidioides* is clearly homologous to the larger groove containing the shell of *Pupillaea annulus*, but it is not as large as that of the latter, and it lacks the shell-secreting outer fold of the mantle that may clearly be seen in the groove of that species after removal of the shell. There is the possibility that specimens identified as *Pupillaea annulus* are but a developmental stage of *Buchanania onchidioides*, but that possibility seems remote, considering that my material of both species appears to be mature. Also, the gill tips in my specimen of *P. annulus* do not project as far as the snout.

CONCLUSIONS

One advantage of the limpet form is that of protection by means of clamping against the substratum. The loss of such capacity is a necessary consequence of shell reduction. All large-bodied fissurellids are unable to tightly adhere and are restricted to low-energy environments, where their prey organisms, sponges and tunicates, flourish. Here the fissurellids have a cryptic form, resembling their prey organisms. Indeed, their habits are more like those of the dorid nudibranchs, which they resemble, than like other limpets.

That the shell in adult members of the *Fissurellidea* group is vestigial, with virtually no function, has been said previously (see Ghiselin, et al. 1975). The truth of this statement may now be illustrated in *Buchanania*, which is comparable to *Fissurellidea* or *Pupillaea* in every respect other than lacking a shell.

The shell is of importance, however, to young stages of the *Fissurellidea* group, considering that juveniles have relatively large shells. Because there is a shell groove in the mature stage and because the species is like *Fissurellidea* in every other respect, it is evident that *Buchanania onchidiodes* must have a shell in its juvenile stage.

A description of juvenile *Buchanania onchidiodes* would be of great interest, to discover how long it persists, and to see if the edge is rounded like that of *Fissurellidea*, or offset, as in *Pupillaea*. I expect it to be offset, in keeping with my hypothesis that *Buchanania onchidiodes* represents the final development in the trend toward shell loss seen in *Pupillaea annulus*.

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Other significant material was contributed by Paul Dayton, Scripps Institution of Oceanography, who collected *Fissurellidea patagonica* in southern Argentina in 1972 and 1973, and C. J. Risso-Dominguez, of Buenos Aires, who collected *Fissurellidea megatrema* in the vicinity of Mar del Plata, Argentina, 1964–1968.

Following my field work in Argentina in 1978 I examined the collections at the Museo Argentino de Ciencias Naturales, Buenos Aires, where access to the collection was facilitated by Martinez Fonte. Other specimens were loaned by William K. Emerson of the American Museum of Natural History.

Carole S. Hickman, University of California, Berkeley, provided the SEM radular illustration of *Fissurellidea bimaculata*. S. Stillman Berry of Redlands, California, loaned his copy of Lesson's "Voyage autour du monde. . . ." Jo-Carol Ramsaran of the LACM Malacology Section assisted with curatorial and library tasks. The LACM photographers and illustrators assisted with preparation of the figures.

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